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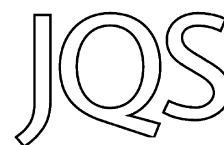
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Drivers of ecosystem and climate change in tropical West Africa over the past ~540 000 years



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ABSTRACT: A paucity of empirical non-marine data means that uncertainty surrounds the impact of climate change on terrestrial ecosystems in tropical regions beyond the last glacial period. The sedimentary fill of the Bosumtwi impact crater (Ghana) provides the longest continuous Quaternary terrestrial archive of environmental change in West Africa, spanning the last ~1.08 million years. Here we explore the drivers of change in ecosystem and climate in tropical West Africa for the past ~540 000 years using pollen analysis and the nitrogen isotope composition of bulk organic matter preserved in sediments from Lake Bosumtwi. Variations in grass pollen abundance (0–99%) indicate transitions between grassland and forest. Coeval variations in the nitrogen isotopic composition of organic matter indicate that intervals of grassland expansion coincided with minimum lake levels and low regional moisture availability. The observed changes responded to orbitally paced global climate variations on both glacial–interglacial and shorter timescales. Importantly, the magnitude of ecosystem change revealed by our data exceeds that previously determined from marine records, demonstrating for the first time the high sensitivity of tropical lowland ecosystems to Quaternary climate change.

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KEYWORDS: Lake Bosumtwi; nitrogen isotopes; orbital forcing; palynology; West Africa.

Introduction

Understanding the relationship between tropical ecosystems and climate in Africa is of critical importance because of the continent's sensitivity to global climate change (IPCC, 2013), the region's high ecological value (Myers *et al.*, 2000) and its role in hominid evolution (deMenocal, 2004). Today, the highly biodiverse tropical West African region is regarded as being particularly vulnerable to impacts from a rapidly growing human population (Lambin *et al.*, 2003), and naturally driven periodic multi-decadal drought (Shanahan *et al.*, 2009). Furthermore, in West Africa, projected regional warming (1–1.5 °C by 2099) threatens the stability of current ecosystems (IPCC, 2013). Little is known, however, about the resilience of the natural vegetation to such high-magnitude climate change.

Quaternary (last 2.6 million years, Ma) records of environmental change in West Africa can provide vital insights into how ecosystems may respond to future climate change because of the comparable magnitude of Quaternary temperature changes (Gosling and Holden, 2011) with those predicted in the coming years (IPCC, 2013). This task is inhibited, however, by an absence of terrestrial successions that reconstruct ecosystem dynamics at a regional scale on long time scales. Rather, marine successions have hitherto formed the basis of understanding Quaternary ecosystem change in West Africa beyond the past ~20 ka (Dupont, 2011). The interpretation of marine records of terrestrial vegetation changes is compromised by uncertainties concerning: (i) wide pollen source areas (comprising both river and aeolian inputs) (Hooghiemstra *et al.*, 2006), (ii) complex oceanic transport pathways, potentially involving offshore

water currents (Hooghiemstra *et al.*, 2006) and (iii) typically low pollen concentrations that may dampen the true variance of terrestrial vegetation change (Dupont, 2011).

The sedimentary fill of the Lake Bosumtwi impact crater (Ghana, West Africa; 6°30'N, 1°25'W; Fig. 1) has yielded the longest Quaternary terrestrial archive of African vegetation to date, spanning the last c 540 ka (Miller and Gosling, 2014). The lake is an ideal site for investigating past vegetation and climatic change because it: (i) has been accumulating sediment over the last 1.08 ± 0.04 Ma (Jourdan *et al.*, 2009), (ii) currently lies just ~400 km south of the savannah to deciduous woodland transition (Fig. 1; Supplementary Fig. S2) (White, 1983), (iii) is hydrologically closed in terms of both surface and groundwater, and therefore lake level is highly sensitive to changes in moisture balance (Talbot and Johannessen, 1992), and (iv) lies within the seasonal migration path of the tropical rainbelt (Nicholson and Grist, 2001; Miller and Gosling, 2014). The large diameter of the Bosumtwi crater (6–11 km) (Koeberl *et al.*, 2005) also means that the majority (>80%) of the pollen accumulating in the sediments throughout the period of deposition is likely to be derived from the regional landscape, following the model of Jacobson and Bradshaw (1981).

Methods

In 2004, 1833 m of sediment was cored from 14 separate drill holes from Lake Bosumtwi by the International Continental Drilling Program (Koeberl *et al.*, 2005). In this study we have used core BOS04-5B (hereafter 5B), which was recovered from the deepest part of the lake (74 m) and yielded the longest sedimentary succession (295 m in length; Koeberl *et al.*, 2005). To reconstruct past vegetation shifts and moisture balance changes we conducted pollen and nitrogen stable isotope ($\delta^{15}\text{N}$) analysis of organic matter on the upper 151 m of 5B (interval studied to date).

Fossil pollen samples ($n=217$, at an average temporal resolution of c. 2.4 ka) from 5B were counted to a minimum of 300 terrestrial pollen grains using a Nikon eclipse 50i

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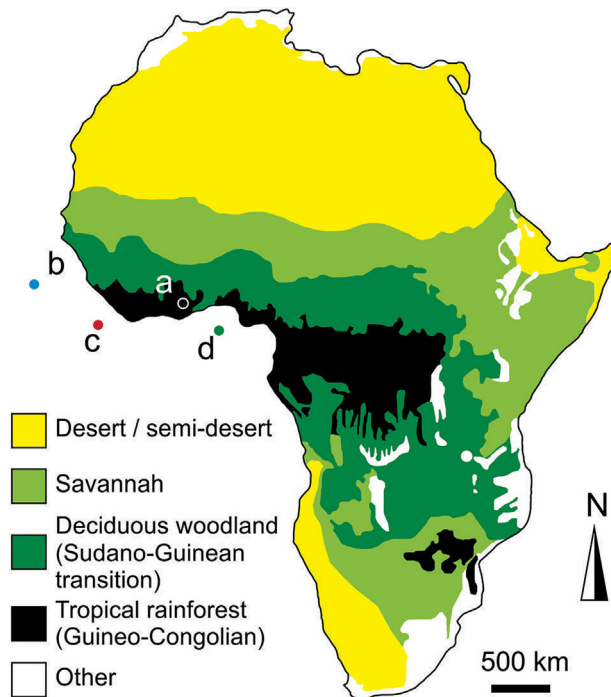


Figure 1. Simplified map of the distribution of modern vegetation biomes across Africa, modified from White (1983). For more detailed biomes and sub-divisions into ecoregions see Fig. S2. Sites discussed are (a) Lake Bosumtwi, (b) GIK16415 (Dupont and Agwu, 1992), (c) GIK16776 (Jahns *et al.*, 1998), (d) GIK16856 (Dupont and Weinelt, 1996).

binocular microscope at a magnification of 40× and 100× (for particular identifications). In total, 216 pollen taxa were identified to at least family level and a further 425 pollen types were categorized. Identifications were based on Gosling *et al.* (2013) and Reille (1995). Pollen concentrations were calculated relative to exotic *Lycopodium* marker tablets (Stockmarr, 1972). Statistical analysis of the fossil pollen assemblage was achieved using the detrended correspondence analysis (DCA) function in Psimpoll (Bennett, 2003). DCA was performed on all pollen samples and including all pollen taxa reaching an abundance of >2% of the pollen sum in at least one sample (43 taxa).

Charcoal concentration was determined in the same samples as counted for pollen and spore analysis. Charcoal fragments above 10 µm in size were counted using a manual cell counter. Charcoal particles were readily identified by their angular structure, opacity and the presence of visible stomata (Fig. S1). Charcoal concentration values were calculated by adding a spike of one *Lycopodium* spore tablet to samples of known volume (Stockmarr, 1972). To ensure sufficient precision was reached, a minimum of 2000 charcoal fragments were counted per sample. The number of *Lycopodium* counted was recorded at 2000 charcoal fragments to calculate charcoal concentration values.

The nitrogen isotope composition of 123 decalcified sample residues was determined at approximately 1.24-m intervals from 150.7 m to core top (at an average temporal resolution of c. 5 ka). Briefly, ~0.6-g sample aliquots were homogenized and treated sequentially with 0.1 M and 1 M HCl for 24 h, before being rinsed to neutrality with Milli-Q water (18.2 MΩ. cm). Each step, involving a change of reagent or water, was preceded by centrifugation (10 min at 1500 r.p.m.) to prevent the loss of fine material in suspension. The nitrogen isotopic composition ($\delta^{15}\text{N}$) of the dried re-homogenized residues was then determined using a Thermo Flash HT elemental analyser

equipped with a Thermo zero-blank device coupled to a Thermo MAT 253 mass spectrometer (EA-MS). Data are expressed following the guidelines for the reporting of stable isotope measurement results (Coplen, 2011); the quantity relative nitrogen $\delta^{15}\text{N}$ is defined by:

$$\delta^{15}\text{N}_{\text{AIR}} = \left(\frac{R(^{15}\text{N}/^{14}\text{N})_P}{R(^{15}\text{N}/^{14}\text{N})_{\text{AIR}}} \right) - 1$$

where R is the isotope-number ratio, $\text{N}(^{15}\text{N})/\text{N}(^{14}\text{N})$, of the two isotopes of nitrogen in specimen P , and the equivalent parameters follow for the international measurement standard Air. The average $\delta^{15}\text{N}$ of IAEA NO3 and the in-house urea standard was $4.6 \pm 0.12\text{‰}$ (1σ) and $-0.9 \pm 0.12\text{‰}$ (1σ), respectively. The measured $\delta^{15}\text{N}$ value for IAEA NO3 is within uncertainty of certified published values ($4.7 \pm 0.2\text{‰}$) demonstrating the accuracy of our protocol. As a true estimate of our precision, six aliquots of sample 52E-1 from 75–75.5 cm (140.6 m composite depth, c. 504.8 ka; Table S1) were analysed, returning a standard deviation of 0.45‰ (1σ). These samples were run on multiple days and consequently represent the uncertainty of the reported $\delta^{15}\text{N}$ of organic residues from Lake Bosumtwi.

Chronological control within core 5B is provided by radiocarbon back to ~47 ka and optically stimulated luminescence (Shanahan *et al.*, 2013b), and a basal Ar–Ar age for the crater impact glass of 1.08 ± 0.04 Ma (Fig. S3). The age model used for the pollen and nitrogen isotope data shown here was derived by linear interpolation of age with depth through the radiocarbon ages to ~47 ka, and then linear interpolation from the oldest radiocarbon age to the basal Ar–Ar age.

Results and discussion

To characterize major ecosystem change (vegetation shifts) around Lake Bosumtwi we examined the fossil pollen record (Figs 2 and 3; Supplementary Table S2). Poaceae (grass family) is the most common taxon in the pollen record of 5B, but shows high variability in abundance through the core, ranging from 0 to 99% of total terrestrial pollen content (Fig. 3). Pollen concentration is high throughout the core (average $35\,300$ grains cm^{-3}) except for 34–33 m, which is effectively barren ($90\text{--}1400$ grains cm^{-3}). A positive correlation ($r=0.67$) between Poaceae and charcoal concentration indicates that the Poaceae is not an aquatic species, but most likely a combustible species from the tropical and subtropical grasslands, savannah and shrublands (Olson *et al.*, 2001; Fig. S1 and Table S2). DCA has been used to characterize the main variance within the fossil pollen dataset (Figs 2 and 3). The pollen taxa identified were classified into ecological groups (phytochoria; Table S2). The weighting of pollen taxa along DCA axis 1 is interpreted as characterizing shifts between savannah ('savannah' phytochoria) and woody species (from the 'deciduous woodland–Sudano-Guinean transition' and the 'tropical and subtropical moist broadleaf forests' phytochoria). Characteristic savannah taxa (e.g. Poaceae, Caryophyllaceae, Amaranthaceae) are separated from characteristic woody taxa (e.g. *Farsetia*, *Alchornea*, *Celtis*, *Macaranga*; Table S2). As Poaceae is present also in the deciduous woodland–Sudano-Guinean transition, the discussion concerning grasslands and forests that follows will use the vegetation classification of Olson *et al.* (2001), where grasslands are 'tropical and subtropical grasslands, savannah and shrublands' and forests are 'subtropical moist broadleaf forests'.

Our data indicate the occurrence of several high-magnitude transitions between grassland and forest (Fig. 3A, B). Notably, between 96 and 58 m (~350–200 ka) there are high-frequency shifts between grassland and forest dominance, culminating in a remarkably stable interval of grassland dominance between 58 and 35 m (~200–130 ka, >80 % Poaceae). These large-scale shifts in vegetation indicate significant and rapid changes in environmental conditions around Lake Bosumtwi. Modern African vegetation associations indicate that typically grassland vegetation requires an average precipitation of <600–2000 mm a⁻¹ and a dry season of 4–8 months. Conversely, forest vegetation requires precipitation ranging from 1000 to >10000 mm a⁻¹ and a dry season of 0–5 months (Table S3; Olson *et al.*, 2001; Miller and Gosling, 2014).

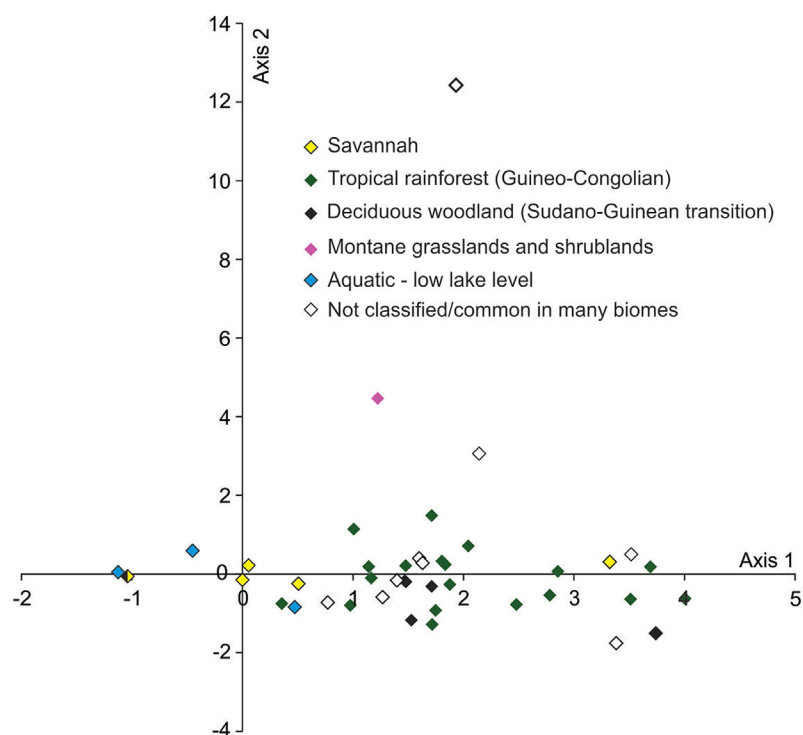
Evidence for pronounced environmental changes in the Lake Bosumtwi record is also provided by our $\delta^{15}\text{N}$ data. $\delta^{15}\text{N}$ values of terrestrial plant material recovered from Lake Bosumtwi range from 4.5 to 10.3‰ (Talbot and Johannessen, 1992; Shanahan *et al.*, 2013a). In contrast, $\delta^{15}\text{N}$ values of aquatic plants in Lake Bosumtwi are higher ($12.8 \pm 0.9\text{‰}$) with a significant contribution from ^{15}N -enriched dissolved nitrogen, produced via denitrification in anoxic bottom waters and upwelled seasonally into the mixed layer (Talbot and Johannessen, 1992; Shanahan *et al.*, 2013a). In core 5B, $\delta^{15}\text{N}$ values of organic matter range from +2 to +14‰ (Fig. 3C). The assimilation and cycling of nitrogen in lakes involves several dissolved inorganic nitrogen (DIN) species. However, in tropical African lakes, during times of stable water column stratification, low DIN concentrations result in an important shift in N cycling by favouring the dominance of cyanobacteria, capable of fixing molecular nitrogen (Talbot and Johannessen, 1992). Organic matter formed via this metabolic pathway typically has $\delta^{15}\text{N}$ values around $0 \pm 2\text{‰}$, similar to that of atmospheric N. Limitation of DIN in Lake Bosumtwi has previously been interpreted as indicative of periods of stable water column stratification, promoted by high lake level (Talbot and Johannessen, 1992; for further information see SOM). Consequently, we interpret decreases

in $\delta^{15}\text{N}$ as indicative of increasing lake levels (Fig. 3C). Importantly, this inference is supported by the close correlation between intervals of low $\delta^{15}\text{N}$ and forest vegetation expansion (Fig. 3), indicating a clear association between forest expansion and enhanced regional moisture availability.

The temporal pattern of vegetation and lake level change in the Bosumtwi record through the last ~540 ka suggests that major ecological and climate oscillations occurred in-phase with orbitally paced Antarctic temperature changes (Fig. 3). Specifically, through most of the Lake Bosumtwi record (notably between ~540 and ~350, and ~130 and 0 ka), oscillations in vegetation and lake-level occurred in-phase with ~100-ka-scale glacial–interglacial climate oscillations (Fig. 3). Spectral analysis of Poaceae abundance, DCA axis 1 and $\delta^{15}\text{N}$ data support this observation, indicating high variance in these records at ~30-m (i.e. ~100-ka) periods (Fig. S4). This interpretation is intuitive as globally warmer interglacial intervals are associated with low grassland abundances from the region, whereas cooler glacial conditions are associated with high grassland abundances (Fig. 3A, B) (Dupont, 2011).

Similar evidence for an orbital control on fossil pollen abundance has been recognized from nearby marine sediment cores (Figs 1 and 4), further emphasizing the link between orbital-scale processes and tropical climate (deMenocal *et al.*, 1993). In comparison with the Lake Bosumtwi record, however, these marine cores do not reveal the true extent of the regional impact of global climate change on West African tropical ecosystems (Fig. 4). Firstly, the inferred vegetation changes from the pollen data of marine cores are of lower magnitude and display only ambiguous correlation with global temperature (Fig. 4). Secondly, the marine records display predominantly gradual vegetation changes rather than the more rapid transitions observable in the Bosumtwi record (Fig. 4). This rapidity may of course be due to possible sedimentary breaks during periods of lake level low-stand; however, the only low-stand that has been identified from the sedimentology occurs between 135 and 75 ka (Scholz *et al.*, 2007). The

Figure 2. Ordination of Lake Bosumtwi fossil pollen DCA taxon scores axis 1 vs. axis 2. Axis 1 represents most of the ecological variance [eigenvalue (EV) 0.44, axis 2 EV is 0.21]. DCA was performed on all pollen/spore taxa reaching an abundance of >2 % of the pollen sum in at least one sample. In total, 43 pollen/spore taxa were included from 217 samples. Ecological groupings follow Table S2 (phytochoria). Note that the savannah species plotting positive on axis 1 is *cf. Securinega*, and although classified by Frédoux (1994) as savannah some species prefer moist soil. Poaceae is grouped into both the savannah and the deciduous woodland phytocoria.



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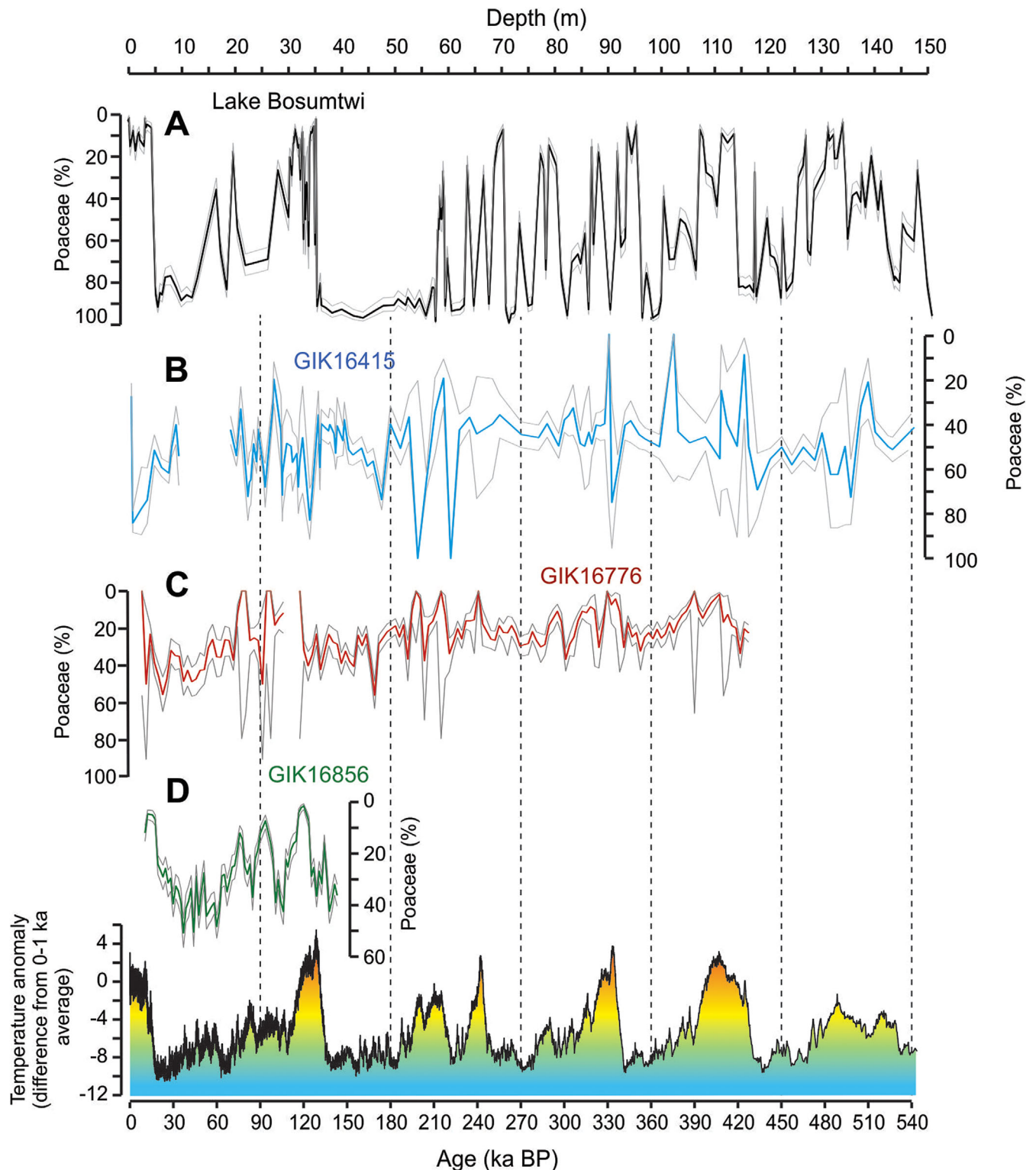


Figure 4. Comparison of Lake Bosumtwi core 5B Poaceae (grass) record with Poaceae records from nearby marine cores. Note that the Bosumtwi record is quantified as percentage abundance relative to total terrestrial pollen abundance. The marine core Poaceae datasets are calculated based on the sum of total pollen and spores and the data are from Pangaea. Locations of alphabetically labelled sites are shown in Fig. 1. Grey lines on each plot are the calculated 95% confidence intervals for pollen percentage data based on Maher (1972). Note the low variability in these marine records relative to the Lake Bosumtwi record.

hypothesis that high-latitude glaciations influenced low-latitude vegetation and climate (Maley and Livingstone, 1983), probably through concomitant fluctuations in Atlantic sea surface temperatures, which mediated the latitudinal displacement of the tropical rainbelt (Weldeab *et al.*, 2007). Importantly, however, comparison of the Lake Bosumtwi record between 96 and 35 m, (~350–130 ka; Fig. 3A, B) with

Antarctic climate (Fig. 3E) suggests high-latitude forcing of West African climate was weaker in this interval, with vegetation changes instead showing rapid fluctuations on shorter (millennial) timescales (Fig. 3A, B). Over this period (~350–130 ka) the strength of orbital precession reached a maximum (Fig. 3D), enhancing low-latitude seasonality and therefore the strength of the West African summer monsoon.

During this interval the seasonal limit of the tropical rainbelt probably moved northward in response to strengthened insolation (Shanahan *et al.*, 2015), which resulted in greater moisture delivery to North Africa during the summer (Larrasoña *et al.*, 2003), but lower rainfall to the south because of the longer summer dry season. This inference is supported by the generally low lake level throughout this interval at Lake Bosumtwi (Fig. 3C), and the broad coincidence between maximum precession amplitude and a long period of grassland stability (58–35 m). The Bosumtwi data indicate that the role of precession in controlling tropical climate (Clement *et al.*, 2004) and vegetation is variable, and dependent upon the Earth's precise orbital configuration.

The ~540-ka sedimentary record from Lake Bosumtwi, Ghana, provides two key new insights into the relationship between global climate and tropical ecosystems. First, regional-scale grassland–forest shifts are approximately twice as large as previously indicated from marine records (meaning we may have previously underestimated the scale of the vegetation shifts), and also include hitherto unrecognized millennial-scale variability. Second, these large-scale vegetation changes can be linked to changes in the global climate system driven by orbital precession, and that the sensitivity of the tropical ecosystem depends on the precise orbital configuration. These insights emphasize the susceptibility and sensitivity of West Africa to large-scale environmental changes, information that is of key importance for the accurate parameterization of climate models and the prediction of future ecosystem development.

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Supplementary Material

Figure S1. The relationship between charcoal and grass concentration, and the relationship between charcoal and total pollen concentration.

Figure S2. Map of present-day ecoregions of West Africa.

Figure S3. Relationship between sediment depth and age for the Lake Bosumtwi 5B sediment core.

Figure S4. Spectral analysis of fossil Poaceae pollen and $\delta^{15}\text{N}$ from Lake Bosumtwi.

Table S1. $\delta^{15}\text{N}$ sample replicate data.

Table S2. Fossil pollen taxa groupings.

Table S3. Modern vegetation of tropical West Africa.

Abbreviations. DCA, detrended correspondence analysis; DIN, dissolved inorganic nitrogen.

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